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Flow Through and Around the Abalone *Haliotis kamtschatkana*

by

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Abstract. Fluorescein dye streams released along the shell and at the shell openings of living and dead abalones revealed the lines of water flow around and through the shell. Regardless of ambient flow speed, water entered the shell of live abalones at a region to the left of the left cephalic tentacle and also through the one or two most anterior shell openings and exited through the two or three most posterior openings. An identical flow pattern occurred through the shell of dead, intact animals when placed in an ambient flow of 6 cm/s, regardless of whether the anterior end faced upstream or downstream. Since the exhalent openings occur at the site of the shell at which the ambient streamlines are maximally compressed, they experience a reduction in pressure relative to the anterior, inhalent ones. Thus, the design of its shell may enable the abalone to take advantage of an induced flow to move water more efficiently through its mantle cavity.

INTRODUCTION

Haliotis kamtschatkana Jonas, 1845, the pinto abalone, must deal with changes in environmental flow while maintaining respiratory currents through its mantle cavity. These animals have a row of four to six openings through the dorsal shell surface that, according to earlier workers (GARSTANG, 1928; CROFTS, 1929; YONGE, 1947) evolved to prevent wastes released in the mantle cavity from moving forward over the gills and head. In addition to creating a flow through its shell by beating the cilia of its gills, *Haliotis* could use environmental currents to help drive water through its mantle cavity. Such an induced flow requires that the inhalent openings encounter fluid at a pressure higher than that of the exhalent openings (VOGEL, 1981). MURDOCK & VOGEL (1978) found that the keyhole limpet, *Diodora aspera,* experiences such an externally driven flow and may use this flow to move water more efficiently through its mantle cavity. *Haliotis kamtschatkana* lives in areas of surge and strong currents (Richard Emlet, personal communication), where it seems possible that its series of shell openings could be exposed to pressure differences sufficient for induced flow to occur. To visualize the paths that lines of water flow follow around and through abalones I combined information from dissections, dye streams, and flow velocity measurements taken in and around living and dead individuals.

MATERIALS AND METHODS

Five adult individuals of *Haliotis kamtschatkana* ranging in maximum aperture diameter from about 9–12 cm and collected from various sites in the Friday Harbor region of San Juan Island, Washington were used. The flow these animals normally encounter may range from 0–150 cm/s or more (Kenneth Collier, personal communication).

To relate the external flow information to the anatomy of the animal, I dissected both fresh and narcotized animals. To narcotize, I added increasing volumes of a 7% $MgCl_2 \cdot 6H_2O$ solution to animals in cooled (8°C) sea water until the epipodial and cephalic tentacles no longer retracted when touched.

To visualize the flow of water qualitatively through and around *Haliotis kamtschatkana,* I used a stream of fluorescein dye controlled by a micro dye injector (an adjustable syringe fitted with a drawn plastic tip and moved by a micromanipulator). Pencil marks at 1-cm intervals along the edge of the shell served as reference points for following dye paths, technically referred to as streaklines. Dye was released at each of these points along both sides of the animals as well as at various sites near the anterior and dorsal surfaces of the shells. Studies of animals in flowing and in still water took place in a 15-cm flow tank designed by VOGEL & LABARBERA (1978).

Observations of induced flow were made on animals

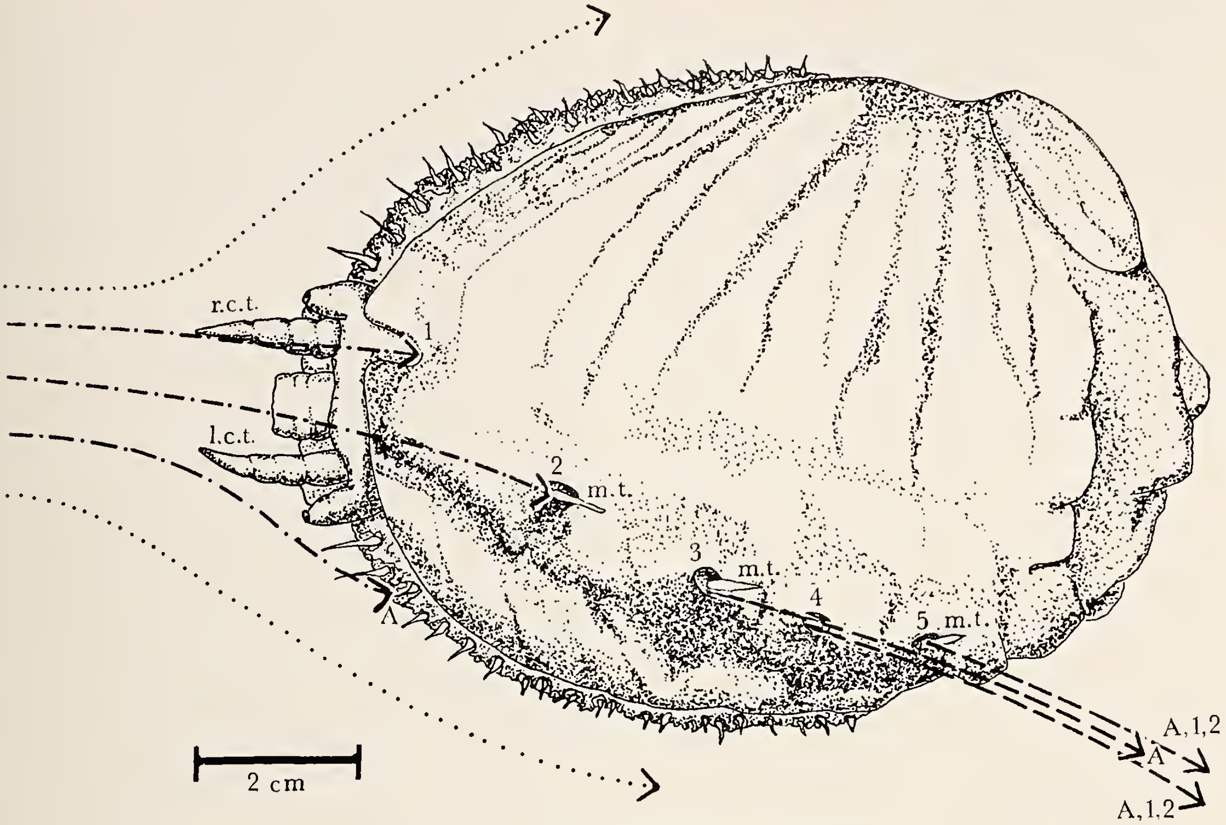

Figure 1

Diagram of flow through and around an abalone facing upstream in an ambient flow of about 6 cm/s. l.c.t.: left cephalic tentacle; r.c.t.: right cephalic tentacle; m.t.: mantle tentacle; A: site at left side of shell where water enters mantle cavity; 1, 2: anterior, inhalent shell openings; 3, 4, 5: posterior, exhalent shell openings; dot-dash lines (–·–·–): inhalent streaklines; dashed lines (– – –): exhalent streaklines; dotted lines (·····): flow along anterior end and side of shell. Letters and numbers at ends of exhalent streaklines correspond to the points at which streaklines may have entered the mantle cavity.

that were first relaxed in $MgCl_2$ as above and then quickly frozen to −20°C by placing them in the bottom of a cryostat. The animals were returned to ambient sea water temperature before any data were taken.

RESULTS

Dye released at specific points around an animal facing upstream in an ambient flow of about 6 cm/s formed a repeatable set of streaklines (Figure 1). Water approaching the anterior edge of the shell was either deflected upward (perpendicular to the general direction of flow), straight upstream (180° to the general flow), or was passed in a series of vortices along either side of the shell. Flow contacting the shell at either side continued downstream close along the shell and then became caught in the turbulent backwash behind the animal. In ambient flows ranging from approximately 2–15 cm/s the streaklines did not appear to be velocity-sensitive, although there was more turbulence at higher speeds.

Abalones accepted incoming water only at specific sites along the shell (Figure 1: A, 1, 2). At the lower edge of the shell, water entered in a region 1–3 cm to the left of the left cephalic tentacle. It appeared that the animals could control the entrance at this region by waving the left cephalic tentacle. Dye released in the region between the two cephalic tentacles sometimes traveled along the edge of the shell, over the left tentacle and eye, and into the mantle cavity. At other times under the same flow conditions it was deflected by the tentacles and passed downstream alongside the shell.

The two most anterior openings of the shell also served as sites of water intake. Depending upon the position of the mantle tentacles, dye released upstream, above, or beside these openings entered the mantle cavity. If the anterior opening was incomplete, resembling a fold at the edge of the shell, dye released just below its dorsal edge proceeded into the mantle cavity, while dye released at other points within the same region traveled up and out away from the shell, as mentioned above.

Only the two or three most posterior openings on the top of the shell served as the animals' exhalent passages from the mantle cavity. In all cases the penultimate opening (4 in Figure 1), which ordinarily has no mantle tentacle, was the chief channel for wastes and exhalent water flow. The most posterior opening was often partially sealed and always had a tentacle, both of which reduced its output volume and rate. The center-most opening, which usually had a mantle tentacle, tended to be weakly inhalent, although at times dye streams also exited from it. Dye streams usually exited from the posterior or from the right side of the exhalent openings and were laminar.

Except at regions of exhalent and inhalent currents, dye released at the sides of animals standing in still water did not move. The inhalent and exhalent regions were at the same locations in animals in still water as they were in moving water.

Dye released at the inhalent openings of dead, intact abalones facing upstream in a flow of about 10 cm/s entered the mantle cavity at the site of release and exited through one of the exhalent openings. Shells of the same animals oriented downstream had similar patterns of flow through them, although the rate of the induced flow was not as high. In either orientation, dye released near exhalent openings did not enter the shell, but continued downstream.

DISCUSSION

Although earlier reports indicated that water enters the abalone mantle cavity only under the margin of the shell and mantle flap on either side of the head (Stephenson, 1924; Crofts, 1929; Yonge, 1947), it is well known now that in at least some species the first hole serves for water intake as well (*e.g.*, Abbott & Haderlie, 1980, p. 233). In *Haliotis kamtschatkana* the streaklines show that flow enters the mantle cavity in a restricted region to the left of the head and through the first, and sometimes second, shell opening. Only the posterior openings are exhalent, and they are the only channels by which water and excretory products may exit the mantle cavity.

The fact that the shell of a dead animal shows flow patterns through its openings similar to those of a live animal suggests that by its design, the animal may take advantage of an induced flow. Because of the shell shape, the exhalent openings lie in the region at which the streamlines over the shell are maximally compressed, leading to a reduction of pressure over the posterior openings relative to the anterior ones, which should cause the fluid to enter at the front and to exit at the rear (Vogel, 1981). Location of openings relative to any wake formed and the geometry of the openings may also determine local pressure, but these aspects of flow were not investigated.

The orientation of the openings may further enhance the induced flow. As openings form at the anterior edge of the shell, they face the oncoming flow when the animal is facing upstream, and thus encounter dynamic pressure, or the pressure created due to stopping fluid (Vogel, 1981). As the shell grows and new openings are added, older openings rotate relative to a horizontal surface, becoming more nearly parallel to flow, so that by the time they reach the central region of the shell and begin to function as exhalent openings they experience the reduced pressure described above. Thus as an animal grows, each opening performs first an inhalent and later an exhalent function. I noticed that on each animal there is one opening (or sometimes two) that may be both slightly inhalent near its anterior edge and exhalent near its posterior edge. Such transitional openings are located on the cusp of the shell and are oriented at an angle intermediate to openings that are strongly inhalent or exhalent. It may be that there is some angle at which an opening may no longer serve as an entrance to, and another at which it may begin to serve as an exit from, the mantle cavity. It is also possible that the cephalic and mantle tentacles may valve the openings and help control the direction and rate of flow.

Since induced flow may occur whether animals are facing upstream or downstream, they may need only be parallel to the general direction of surge to take advantage of it. This would make induced flow useful in regions of surge where flow reversal is common. It would be valuable to know if abalones orient to flow in their natural habitat and to what degree orientation is necessary for utilizing induced flow.

Traditionally, workers have believed that the openings in an abalone's shell evolved primarily as a way to avoid mixing fresh inhalent water with waste-laden exhalent water. I have shown that in addition to eliminating this problem, the shell determines the path by which water will enter, as well as exit, the mantle cavity. Whether or not this design increases the efficiency of moving water through the mantle cavity will require a study of the energetics of water movement.

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